

LIOCHELES LITODACTYLUS (SCORPIONES: LIOCHELIDAE): AN UNUSUAL NEW
LIOCHELES SPECIES FROM THE AUSTRALIAN WET TROPICS (QUEENSLAND)

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Monod, L. & Volschenk, E.S. 2004 06 30: *Liocheles litodactylus* (Scorpiones: Liochelidae): an unusual new *Liocheles* species from the Australian Wet Tropics (Queensland). *Memoirs of the Queensland Museum* 49(2): 675-690. Brisbane. ISSN 0079-8835.

A new scorpion species, *Liocheles litodactylus*, is described from the Thornton Uplands, a small mountainous massif of Far North Queensland, Australia. This species differs most notably from all other species of the genus by the absence of a lobe on the movable pedipalp finger and of a corresponding notch on the fixed finger in both males and females. Comments concerning the taxonomic value of this feature within Liochelidae are given. *Liocheles litodactylus* is the first Australian scorpion that can be considered to be a short range endemic species and additional notes are given on the probable mechanism by which this species evolved. □ *Liocheles litodactylus*, Liochelidae, Scorpiones, endemic, Wet Tropics, Queensland.

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In a landmark revision of the Australo-Papuan scorpion fauna, Koch (1977) recognised 3 species in *Liocheles*: *L. australasiae* (Fabricius, 1775), *L. karschii* (Keyscriling, 1885) and *L. waigiensis* (Gervais, 1843). Additions to the Australian fauna since then are *Liocheles extensus* Locket, 1995 (Locket, 1997) from Kakadu National Park (Northern Territory) and *Liocheles polisorum* Volschenk et al., 2001, the only known cave-adapted species in the family, from limestone caves of Christmas Island (Indian Ocean).

Liocheles australasiae is widely distributed from India to the western Pacific Islands and can be easily distinguished from all other Australian *Liocheles* by its trichobothriotaxy (Fig. 1): the trichobothrium *Esb* is positioned basally, close to the *Eb* group, whereas in the *L. waigiensis* group, it is located more distally, closer to *Est*. The wide distributional range of *L. australasiae* is significant in that it crosses Wallace's Line (and all other noted biogeographical lines in the Indopacific region), an impressive distribution considering the relatively low vagility of scorpions. The ability for this species to disperse and colonise islands in the region has been documented by its appearance on Sertung (Vachon & Abe, 1988), an island remnant of the Krakatau Island (a volcano), destroyed and fragmented during its eruption in 1883. In 1952 Anak Krakatau, the new volcanic cone of former Krakatau, erupted violently and is thought to have eliminated any previously existing scorpion populations on the island group (Vachon & Abe, 1988). Surveys

conducted prior to the 1952 eruption of Anak Krakatau, in 1908 (Jacobson, 1909) and 1933 (Kopstein, 1935), did not find *L. australasiae*. The population reported by Vachon & Abe (1988) can therefore be attributed to a recent colonisation event.

Liocheles waigiensis, the most commonly encountered species in Australia, is widely distributed in tropical and subtropical forests along the north-eastern coast (Queensland and the north of New South Wales). *Liocheles waigiensis* is also reported from rainforest patches in the Northern Territory and even in relictual rainforest patches of the Kimberley region of Western Australia. This species was considered polymorphic by Koch (1977). However, Monod (2000) indicated that several morphologically discrete forms are included under *L. waigiensis* and the species is likely to be subject to splitting in the future.

In Australia *L. karschii* is confined to Cape York Peninsula and to various islands in the Torres Strait, but it also occurs in southern New Guinea (Koch, 1977; Seymour et al., 1995).

An ongoing revision of all *Liocheles* species indicates that *L. waigiensis*, formerly considered as polymorphic (Koch, 1977), is composed of several distinct species. In this contribution, we describe *L. litodactylus*, a new species from the Queensland Wet Tropics.

Mature males of *Liocheles* typically possess an apophysis on the movable chela finger, whereas juveniles and females do not. *Liocheles litodactylus* shows a feature unique among the known *Liocheles*

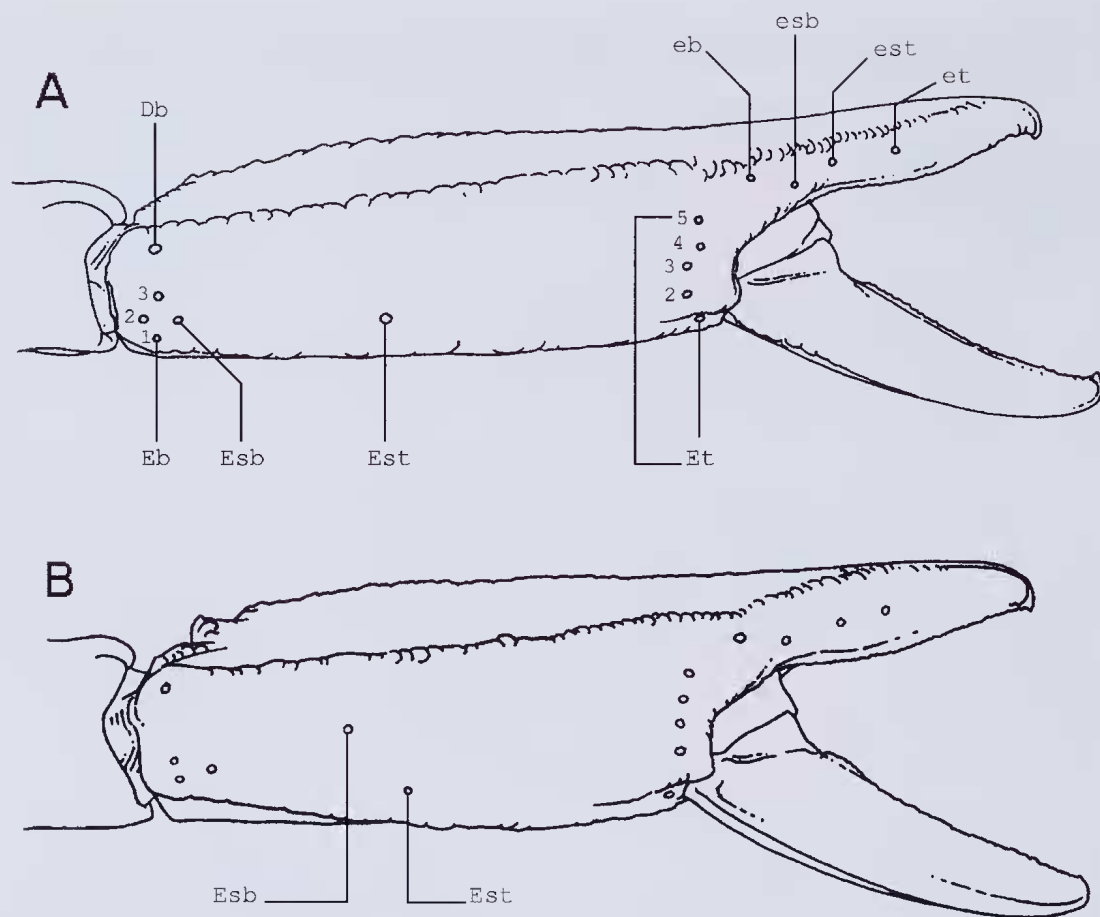


FIG. 1. Trichobothriotaxy of the external face of the pedipalp chela; A, *Liocheles australasiae*; B, *Liocheles waigiensis*.

species: both males or females possess pedipalp fingers without any tubercular sculpturing on the dentate margins. The morphology of pedipalp fingers sculpture has previously been considered as an important phylogenetic and taxonomic feature within the family Liochelidae (Newlands & Prendini, 1997; Prendini, 2000, 2001), but this is the first case in which this character is found to be important for species determination within *Liocheles*.

MATERIAL AND METHODS

Illustrations were produced by using a Wild M5 stereomicroscope with a drawing tube. Trichobothrial notations and terminology of metasomal carination follow those of Vachon (1974), measurements follow those of Stahnke (1970) and are in mm. Additional morphological terminology mostly follows that of Hjelle (1990) and

Sissom (1990), and terminology of pedipalp chelal carination follows that of Prendini (2000). Hemispermaphore terminology is modified from the terminology applied by Lamoral (1979) and the terms used here are explained in the text and in Fig. 5. A more detailed examination of hemispermaphore morphology of scorpions is currently undertaken by Volschenk (in prep). The distribution map was generated with ArcView® GIS 3.1 and maps and drawings were edited in Adobe Illustrator® 8.0.

Family LIOCHELIDAE Fet & Bechly, 2001

DIAGNOSIS. Based on Lourenço (1989) and Prendini (2000). Vesicular bulge absent; cheliceral coxae lacking scaphotrix (stridulatory setae) or trichopae (chemoreceptive lamelliform setae); pedipalp chela with trichobothrium *Dt* located medially (or approximately so) on the

manus, except in *Opisthacanthus* Peters, 1861, in which *Dt* is located proximally on the manus; *Est* located submedially on manus; *eb* on the distal end of the manus, adjacent to the articulation between movable finger and manus; leg tarsi with straight laterodistal lobes; prolateral pedal spur present, retrolateral pedal and tibial spurs absent; metasomal segments I-IV with 2 parallel ventral keels; 2 or 3 pairs of lateral eyes present.

REMARKS. Fet & Bechly (2001) proposed *Liocelidae* as a replacement for *Ischnuridae* Simon, 1879, to resolve the homonymy with the damselfly (Odonata) family *Ischnuridae* Fraser, 1957 (ICZN, 2003).

The distribution of *Liocelidae* is East Gondwanian, with most extant representatives found in Africa, Australia, India and Southeast Asia. However, the liocelid *Opisthacanthus* is found in Africa and in northern South America. This disjunct transatlantic distribution has sparked considerable interest among scorpion specialists, and has resulted in several conflicting hypotheses about the origin of these Neotropical species (Francke, 1974; Lourenço, 1989; Nenilin & Fet, 1992; Newlands, 1973). Unfortunately none of these hypotheses are based on phylogenies determined by using cladistic analyses of morphological or molecular evidence. Prendini (2000) carried out a major cladistic examination of the Scorpionoidea to test the monophyly of scorpionoid families, sub-families and their component genera. This analysis which included exemplar species of all recognised liocelid genera found weak support for all these taxa except for *Liocheles* and *Hadogenes* (Prendini, 2000: figs 2, 5, 6). It emphasised the need for a more comprehensive cladistic study, of all liocelid species to clarify relationships within *Liocelidae*, to establish monophyletic clades and to infer biogeographic hypotheses about the family and its members.

Liocheles Sundevall, 1833

Scorpio (*Liocheles*) Sundevall, 1833: 31. [Type species by monotypy: *Scorpio australasiae* Fabricius, 1775].

Ischnurus C.L. Koch, 1837: 37, pl. VI, fig. 69. [Type species by subsequent designation (Pocock, 1902: 364): *Ischnurus complanatus* C.L. Koch, 1837 (junior synonym of *Liocheles australasiae* (Fabricius, 1775), originally described as *Scorpio australasiae* Fabricius, 1775)] [synonymised with *Hormurus* Thorell by Pocock, 1902: 364].

Hormurus Thorell, 1876: 14. [Type species by original designation: *Ischnurus caudicula* C.L. Koch, 1867 (junior synonym of *Liocheles waigiensis* (Gervais, 1843), originally described as *Scorpio* (*Ischnurus*) *waigiensis* Gervais, 1843)] [synonymised by Karsch, 1880: 408].

Hormiops Fage, 1933: 30. [Type species by monotypy: *Hormiops davidovi* Fage, 1933] [synonymised by Prendini, 2000: 72].

DIAGNOSIS. Pectines with 4-12 teeth; dentate margin of the movable pedipalp finger with 2 parallel longitudinal rows of primary granules regularly interspersed with larger granules and without any accessory granules; ventral surface of leg tarsi with 2 ventral rows of 3-5 acuminate macrosetae, retrolateral row sometimes with one or 2 small basal spinules, ventromedian series of spinules absent; trichobothria in a type C configuration, trichobothriotaxy orthobothriotaxic or neobothriotaxic (patella with 5 trichobothria instead of 3 in *Liocheles penta* Francke & Lourenço, 1991); distal lamella of hemispermatophore 'relatively' short, generally equal in size to the trunk (basal part), with a hook located basally.

REMARKS. Species of *Liocheles*, typical inhabitants of humid and tropical to subtropical ecosystems, are widely distributed in between India and Australia, and throughout the Indo-Pacific and Western Pacific islands. Monod (2000) divided *Liocheles* into 2 distinct species groups, the *L. waigiensis* and *L. australasiae* species groups, on the basis of the trichobothrial pattern on the external side of their pedipalpal chela (Fig. 1).

Liocheles litodactylus sp. nov.

(Figs 2-8)

ETYMOLOGY. Greek, *litos*, plain and *daktylos*, finger; referring to the absence of a lobe on the pedipalp movable finger and of the corresponding notch on the fixed finger in males. Males of all other known *Liocheles* species possess distinctive sculptures on the dentate margins of the chela fingers.

MATERIAL EXAMINED. All known specimens are in the Queensland Museum, and were collected from the Thornton Uplands, NE Queensland, Australia (Fig. 8). HOLOTYPE. ♂, S48320, Mount Pieter Botte, 16°04'S 145°24'E, 950m, 21.XI.1993, G.B. Monteith, H.A. Janetzki, L. Roberts and D.J. Cook. Paratype. S22452, 3 ♀♀: same data as holotype. S35476, 2 ♀♀ Mount Pieter Botte, 16°04'S 145°24'E, 800-900m, 9.XII.1993, G.B. Monteith. S35475, 1 ♂, 2 subadult ♂♂, 1 ♀: Roaring Meg Valley, 16°04'S 145°25'E, 720m, 22.XI.1993, G.B. Monteith, H.A. Janetzki, L. Roberts & D. Cook. Additional Material. S17171, 1 subadult ♀, Granite Outcrops, 0.5km E Mount Pieter-Botte, 780m, 5.X.1982, leg. G.B. Monteith & D. Yeates. S48321, 1 ♂, Mount Halcyon, 16°03'S 145°45'E, 870m, 22-24.XI.1993, G.B. Monteith, D. J. Cook, H.A. Janetzki & L. Roberts. S22453, 1 ♀, 2 ♂♂ subadults, 1 ♂ juvenile, same data as S48321. S35474, 3 ♂♂, 2 subadult ♂♂, Mount Hemmant, 16°07'S 145°25'E, 1050m, 25-27.XI.1993, G.B. Monteith, D. J. Cook, H.A. Janetzki & L. Roberts. S17194, 1 ♀: Thornton Peak, via Daintree, 200-900m, 27.IX.1984, G.B. & S.R. Monteith.

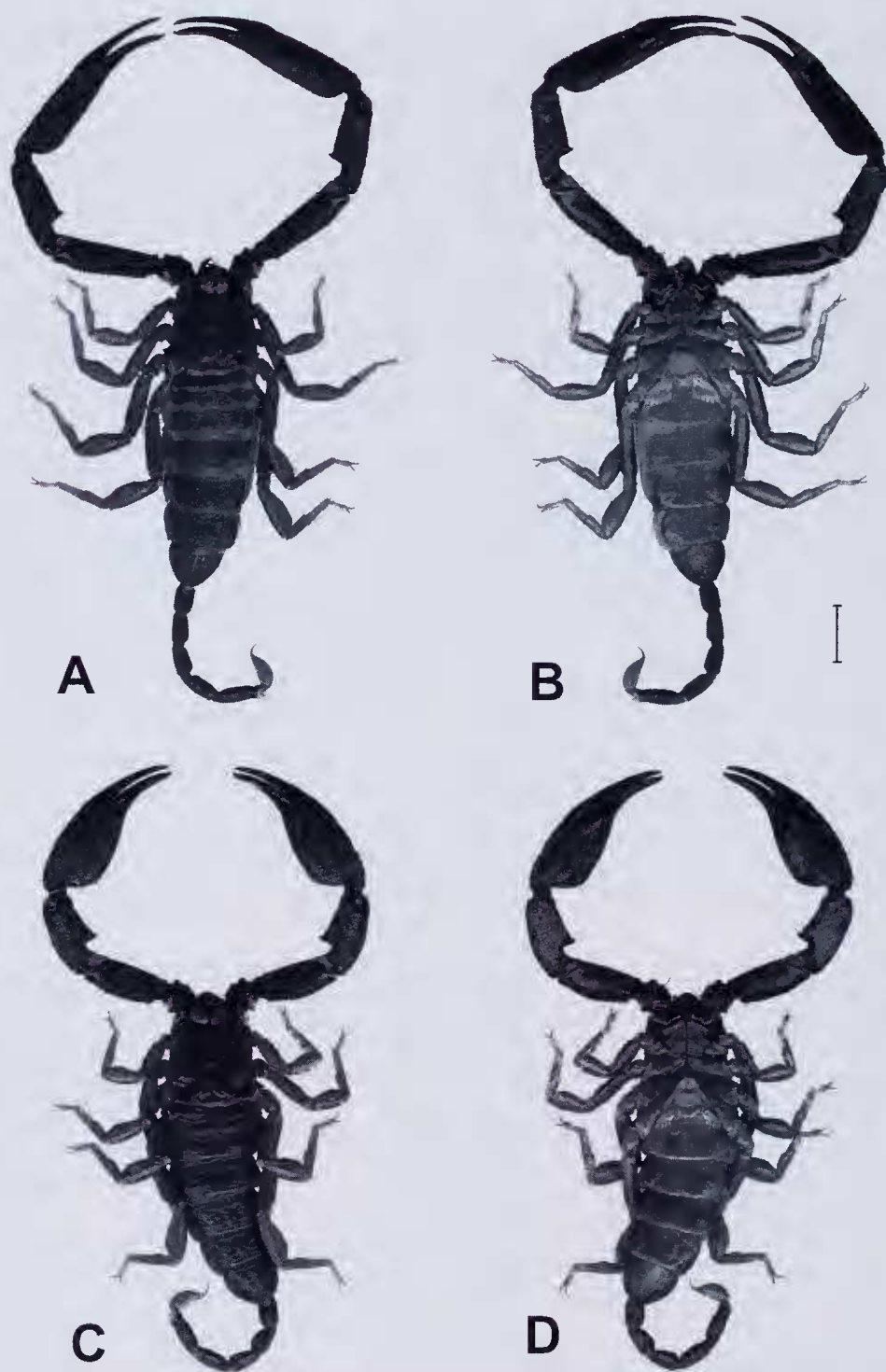


FIG. 2. *Liocheles litodactylus*, male holotype (QMS48320). A, whole animal, dorsal aspect. B, ventral aspect. Female paratype (QMS22452). C, dorsal aspect. D, ventral aspect.

DIAGNOSIS. Dentate margins of the pedipalp chela fingers lacking sculpture in males (Figs 4, 5B) and females.

DESCRIPTION. *Adult Male* (Figs 2A,B; 3A-D; 4; 5B; 6A; 7). *Measurements (holotype).* Carapace, length 6.6, posterior width 7.6; interdistance between anterior lateral eyes 3.4, between posterior lateral eyes 4.5, between median eyes 0.4; diameter of median eyes 0.4. Pedipalp, femur length 10.5, width 2.7; patella length 9.4, width 2.9, chela length 17.9; manus length 10.6, width 2.8, depth 2.4; movable finger length 8.3; fixed finger length 6.0. Metasoma, segment I length 2.4, width 1.7; segment V length 4.4, width 1.2, depth 1.2; vesicle length 4.3, width 1.3, depth 1.4, aculeus length 1.3. Total length 46.5.

Carapace (Fig. 3A). Colouration mostly uniformly tan-brown, with darker brown markings on anterior margins and around median ocular tubercle; posterior and lateral surfaces with faint to distinctive brown reticulate markings; posterior and lateral margins lighter tan with fewer dark markings than on lateral surfaces; median and lateral ocular tubercle blackish brown. Carapace strongly flattened; median ocular tubercle weakly developed, low; sides nearly parallel in the posterior half, convergent in anterior half; frontal concavity or notch moderately developed; anterior lobes rounded; lateral ocular tubercles with 3 ocelli of equal size. Carapace with numerous fine granules and very few nongranular areas; inter-ocular triangle area shagreened; lateral surfaces with both smooth and shagreened patches; anteromedian furrow narrow, suturiform, anteriorly bifurcated; median longitudinal furrow shallow, continuous from the anterior suture furcation, running through ocular tubercle posteriorly into a shallow, smooth and shiny triangular depression; posterolateral furrow shallow, smooth and shiny; mesolateral furrow weakly developed, almost absent.

Mesosoma. Tergite colouration tan-brown with darker brown markings, similar to or slightly lighter than those on carapace; tergite VII slightly darker than other tergites. Tergites I-VI with median carina reduced to a weak non-granular ridge surrounded by a pair of shallow, smooth submedian depressions; lateral carinae absent. Tergite VII with median carina and submedian depressions weakly pronounced, almost absent; lateral and sublateral carinae absent. Surface of tergites predominantly shagreened with scattered granules; possessing a subreticulate formation of low ridges forming numerous irregular shallow

dimples; median area of tergites I-III smooth, without granules and minutely pitted; tergites IV-VII with few tiny smooth patches in median area (patches strongly reduced on most posterior tergites); pre-tergites smooth, shiny and minutely pitted. Sternite colouration pale brownish cream anteriorly, becoming progressively darker posteriorly (to pale brown or tan). Sternites III-VI smooth, shiny and minutely pitted, without granulation or carinae. Sternite VII with similar surface texture as on preceding sternites, except for posterolateral region, coarsely textured and slightly shagreened with few small granules; reduced pair of median carinae present in the posterior region; lateral carinae absent. Spiracles of book lungs crescent-shaped.

Metasoma (Fig. 3D). Short and narrow, shagreened, with scattered granules. Colour tan-brown with numerous subreticulate dark brown markings, fewer markings on dorsolateral surfaces. Segments I-IV with longitudinal dorsomedian furrow and without dorsal, dorsolateral and lateral carinae. Segment I: ventrolateral carinae absent, paired ventral carinae reduced to smooth ridges with tuberculate granules in posterior half. Segment II without ventrolateral carinae, indicated only by a row of few scattered granules; paired ventral carinae reduced to ridges with tuberculate granules on posterior half. Segments III-IV without ventrolateral carinae, indicated only by a row of few scattered granules; paired ventral carinae reduced to ridges with few scattered granules along whole length of segment. Segment V without ventrolateral keels; ventromedian carina reduced to a row of few scattered granules.

Telson (Fig. 3D). Vesicle pale yellowish tan; aculeus darker tan due to stronger sclerotisation; vesicle elliptical or ovate; ventrolateral furrows absent; ventromedian ridge absent; lateral surfaces smooth, nongranular and minutely pitted. Macrosetae very sparse basally, becoming more numerous near base of aculeus. Aculeus stout (equal to or shorter than vesicle depth), moderately curved.

Chelicerae (Fig. 3B). Colour pale yellowish tan; manus without markings basally, with fine dark reticulation in distal half merging with large distal brown patch extending onto basal half of fixed finger; fixed finger dark brown in basal two thirds, becoming lighter internally and distally. Typical tooth arrangement of Scorpionidae (see Vachon, 1963); fixed finger with median and basal teeth bifid; movable finger with one subdistal tooth and one basal tooth in external series; distal external tooth smaller than distal

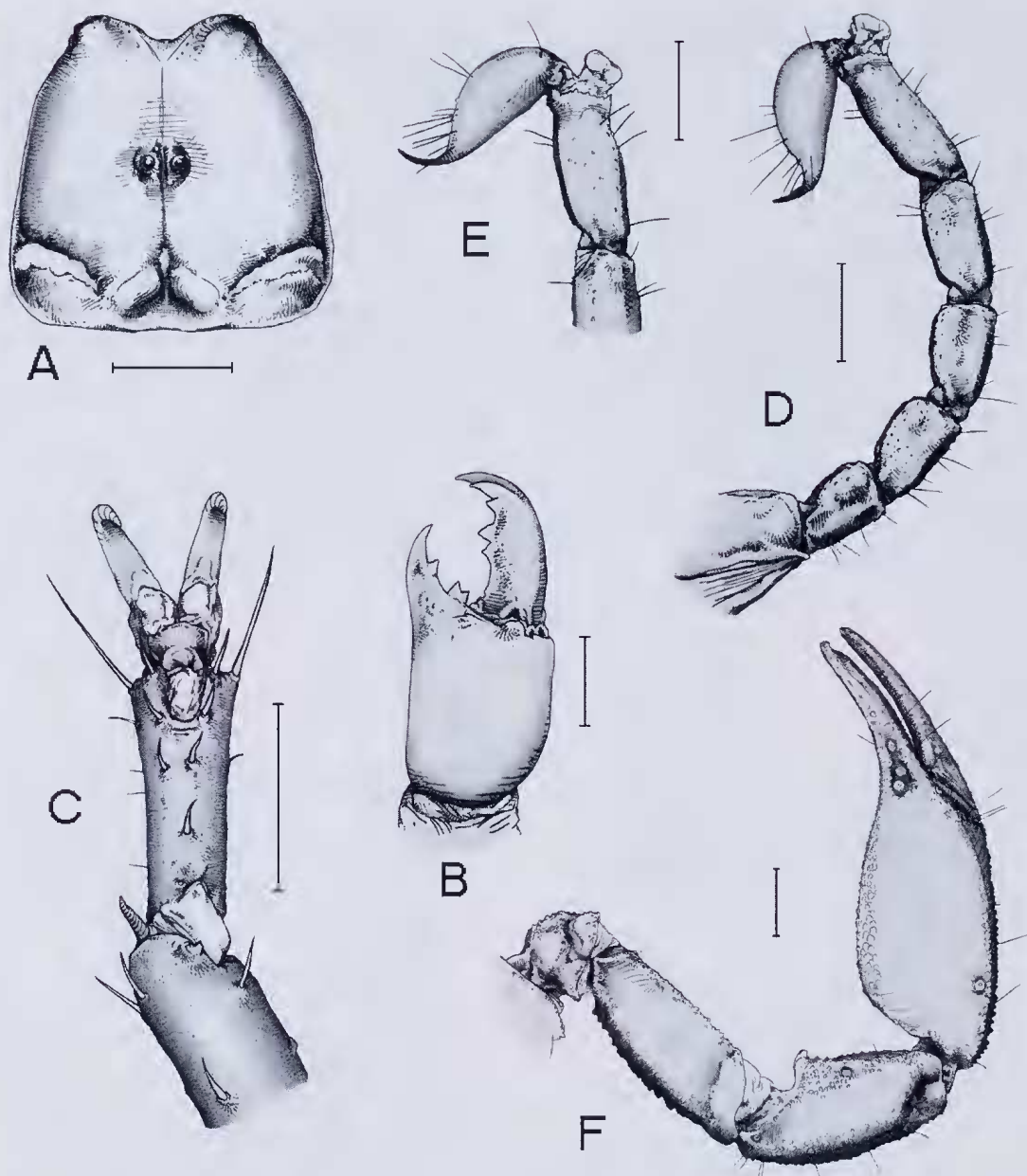


FIG. 3. *Liocheles litodactylus*, male paratype (QMS35475). A, carapace, dorsal aspect. B, right chelicera, dorsal aspect. C, left tarsus IV, ventral aspect. D, metasoma, lateral aspect. Female paratype (QMS35476). E, metasomal segment V and telson, lateral aspect. F, pedipalp, dorsal aspect. Scale lines: A, D-F, 2.5mm; B, C, 1mm.

internal tooth; cheliceral teeth without secondary serrations.

Pedipalp Coxa and Femur (Fig. 4D-F). Pedipalp slender and elongated. Coxa with internoventral

margin strongly granular. Dorsal surface of femur predominantly dark tan brown, internal margins distinctly blackish, external and basal margins less intensely blackish, distal margin with only fine black markings; internal surface

entirely blackish; external surface with only ventral margin blackish; ventral surface with internal, external and basal margins blackish. Femur slender, elongate (length equal to or longer than $3 \times$ the width), pentacarinata, with 4 distinct carinae; internodorsal carina developed as a strongly and densely granular ridge, granules coarse; externodorsal carina reduced to a slightly raised row of scattered coarse granules; interno-ventral carina developed as a weakly granular ridge; extenroventral carina developed as a weakly granular ridge with few strongly developed spiniform granules; ventromedian carina reduced to few granules and confined to base of femur. Dorsal surface shagreened, finely and densely granular, distal end smooth, minutely pitted, without granules; internal surface shagreened, sparsely granular; external surface smooth; ventral surface smooth and sparsely granular, distal quarter minutely pitted, without granules. A total of 3 trichobothria present; *d* located externobasally on dorsal surface; *i* located dorsobasally on internal surface; *e* located dorsobasally on external surface.

Pedipalp Patella (Fig. 4D-F). Slender (length less than $2.5 \times$ the width). Colour predominantly dark tan-brown with black markings; dorsal surface with internal and external margins distinctly blackish, distal end blackish red; internal surface completely blackish; external surface with blackish margins; ventral surface with internal and external margins distinctly blackish, distal end light brown, almost yellow. Seven carinae present, 6 of them distinct; internodorsal carina developed as a ridge of coarse granules with few larger spiniform granules; externodorsal carina weakly developed, reduced to a row of scattered coarse granules; interno-ventral carina developed as a strongly granular ridge (spiniform granules); extenroventral carina developed as a strongly granular ridge (coarse granules); externomedian carina developed as a raised darker row of coarse granules. Dorsal surface shagreened and coarsely granular, with smooth and shiny patches, distal end smooth, minutely pitted, without granules; internal surface shagreened and finely granular; external surface shagreened with a few scattered granules; ventral surface smooth and shiny with a sub-reticulate formation of shagreened and low granular ridges, distal end minutely pitted, without granules. Internal protuberance pronounced, trifold (internal, internodorsal and internoventral tubercles fused into a single large spur). A total of 19 trichobothria present; *d₁* located basally,

external to internodorsal carina; *d₂* located in the distal half of patella; *d₃* absent; *i* in distal third of patella, located dorsally on internal surface. External (*e*) trichobothrial group discernible and orthobothriotaxic: *eb* group composed of five trichobothria, *esb* group of two trichobothria, *em* group of two trichobothria, *et* group of three trichobothria; *est* very close to *em* group. Ventral (*v*) group orthobothriotaxic, three trichobothria.

Pedipalp Chela Manus (Figs 4A-C; 5B). Colour predominantly dark reddish brown with black markings; dorsal surface with internal and external margins distinctly blackish, distal end blackish; internal surface blackish red, median carina black; external surface dark red with blackish margins; ventral surface with external margins distinctly blackish, distal end dark red, almost black. Chela slender (length more than $4 \times$ the width) with five clear carinae; internodorsal carina continuous with low spiniform granules; subdigital carina absent; externodorsal carina distinct, visible as a strongly granular ridge of coarse granules; digital carina well-developed, granules extending from externodorsal carina onto fixed finger; dorsal secondary carina (dorso-median) much reduced, very weakly indicated by larger granules in basal three quarters of manus; internoventral carina continuous, visible as a row of scattered coarse granules; extenroventral carina continuous, crenulate with well developed granules, running parallel to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed between external and internal movable finger condyles; ventromedian carina poorly developed, reduced to scattered granules (more numerous basally); internal (internomedian) carina and external (extenro-median) carina slightly distinct, visible as raised rows of coarse granules highlighted by a dark line. Dorsal surface smooth and shiny, with numerous coarse granules surrounded by small shagreened areas; internal surface sparsely granular with a denser patch of coarse spiniform granules dorsodistally; external surface shagreened with coarse spiniform granules; ventral surface smooth, with few scattered granules, distal end minutely pitted, without granules. A total of 16 trichobothria present; *Db* trichobothria located basally on external surface; *Dt* located on dorsal surface, in basal third of manus; *Eb* group (3 trichobothria) orthobothriotaxic, located basally on external surface; *Esb* located approximately midway between *Eb* group and *Est*; *Em* absent; *Est* located

submedially; *Et* group composed of five trichobothria, *Et*₁ located ventrally; *V* group comprising 4 trichobothria, *V*₃ and *V*₄ located in the basal third of manus, *V*₁ and *V*₂ located in the distal quarter; dorsal trichobothrial salcus undivided, encircling *db*, *dsb* and *dst*; undivided manus salcus encircling *Et*₂₋₄, and *Eb*₅ narrowly connected to external finger salcus.

Pedipalp Chela Fingers (Figs 4A-C; 5B). Basally black, becoming gradually lighter (blackish red) distally, tips of fingers tan brown. Dorsal surface with basal half of fingers shagreened and granular, distal half smooth, shiny, with a few punctations; ventral surface predominantly smooth, shiny and minutely pitted. Fingers without distal diastema [A distinct non-granular and non-denticular space between the most distal granule of the denticular row/rows and the terminal tooth of the chela finger. This character occurs in *Heteroscorpion* (*Heteroscorpionidae*), previously considered a *liocheleid* (*ischnurid*) (Lourenço, 1985, 1989).]. Tips of fingers with pronounced distal hook; denticular margins straight. Fixed finger without basal concavity or any lobe. Movable finger without sculpturing on denticular margin; base of external surface with a group of 3 to 4 (usually 3) whitish spots with glandular appearance. A total of 10 trichobothria present; *db* and *dsb* in very basal portion of finger, on dorsal surface; *dst* in basal half of finger; *dt* located submedially on finger, on internodorsal surface of finger; *eb* in very distal portion of manus, near base of fixed finger, located basally to *db*; *esb* in far distal portion of manus, near base of fixed finger, opposite *dst*; *est* in basal portion of finger, between *dst* and *dsb*; *et* submedially on

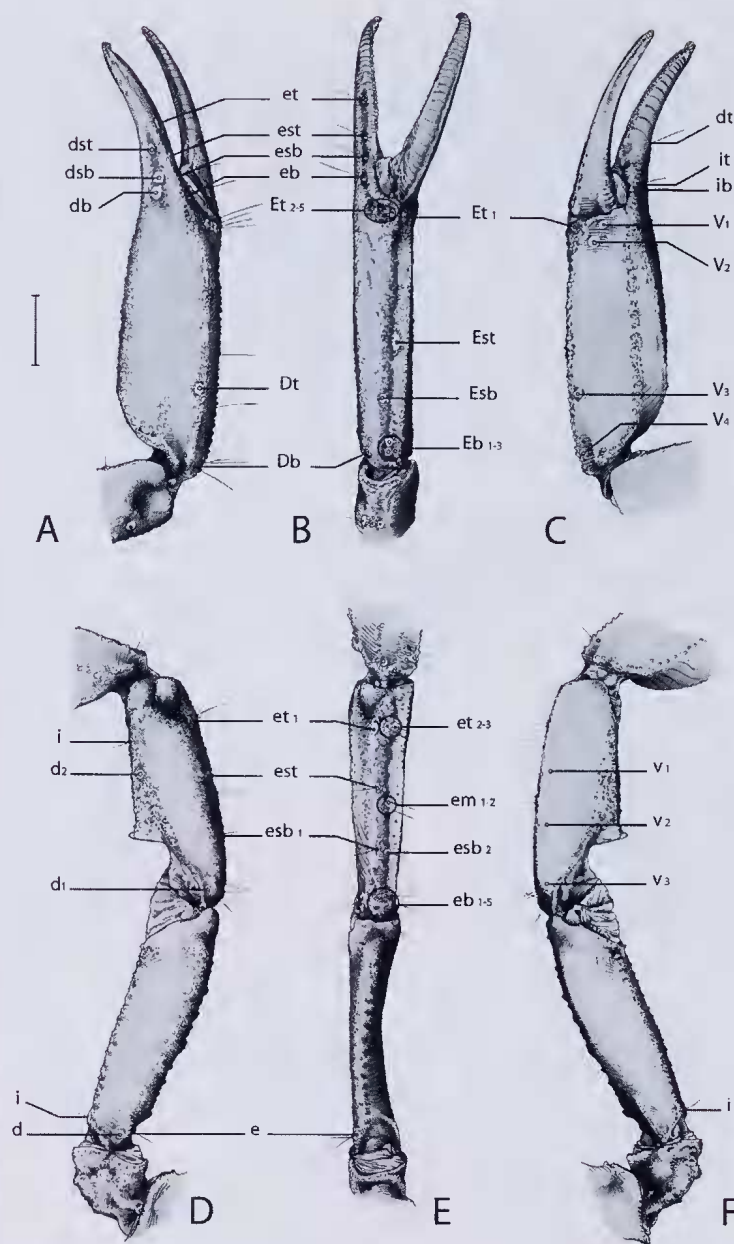


FIG. 4. *Liocheles litodactylus*, male paratype (QMS35475), pedipalp with trichobothrial pattern, chela. A, dorsal aspect. B, external aspect. C, ventral aspect. Femur and patella. D, dorsal aspect. E, external aspect. F, ventral aspect. Scale line 2.5mm

finger, distal to *dst*, opposite *dt*; *it* and *ib* located in distal portion of manus, proximal to base of fixed finger, on internal side of manus; salcus of external finger divided into 2 parts between *eb* and *esb*.

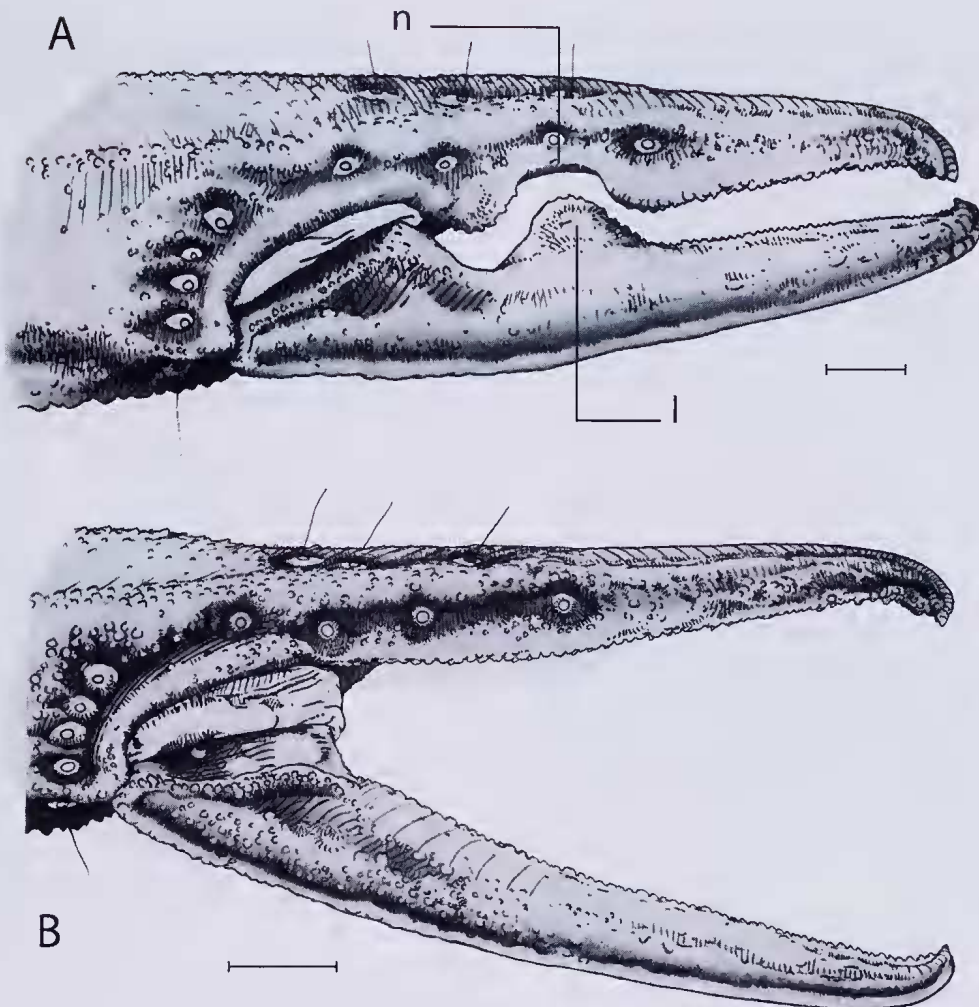


FIG. 5. External aspect of pedipalp chelae fingers. A, male *Liocheles* sp. from Hinchinbrook Island, North Queensland (QMS23260). B, male *L. litodactylus* (QMS35475). Note the presence of a lobe (l) on the movable finger and of a corresponding notch (n) on the fixed finger in A, and the lack of these structures in B. Scale lines 1mm.

Coxosternal Sclerites. Pale yellowish tan to orange; smooth and minutely pitted. Coxapophysis I with anterior margin slightly granular, expanded but not sub-triangular in shape. Sternum of type 2 (Soleglad & Fet, 2003), sub-pentagonal, smooth and minutely pitted; median furrow very shallow, present only in posterior half; posterior pit absent.

Legs. Pale yellowish tan; dorsal surfaces of coxa, trochanter, femur and patella with tan brown subreticulate markings; dorsal surfaces of tibia and basitarsus with distal ends tan-brown; internal margin of femur darker brown. Dorsal

surfaces of trochanter, femur and patella shagreened and sparsely granular; ventral surface smooth, shiny and minutely pitted. Tarsi without ventromedian row of setae and with 2 rows of ventral macrosetae, prolateral row with 3 macrosetae, retrolateral row with 4 macrosetae, one or 2 spinules at base (usually a single spinule present); setae coarse and acuminate; tarsal claws of equal length.

Pectines and Genital Operculum (Fig. 6A). Colour pale yellowish tan, without dark markings; genital operculum composed of 2 triangular plates; genital papillae short, not or

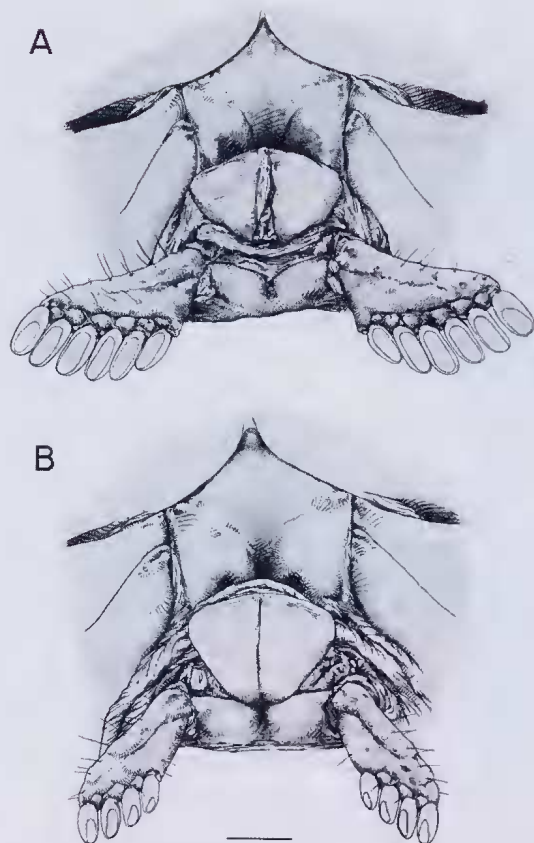


FIG. 6. *Liacheles litodactylus*, pectines and genital opercula. A, male paratype (QMS35474). B, female paratype (QMS35476). Scale line 1mm.

only slightly protruding from beneath operculum; pectines with 6/6 teeth.

Hemispermaphore (Fig. 7). Lamelliform with complex capsule; distal lamellum stout, distally rounded, with a small hook, flagellum length approximately equal in length to that of a capsule region; distal crest absent. Single lamellar hook (h) located below distal lamella base, visible as a short tuberculate protrusion. Distal transverse ridge (Tr) costate, distally strongly curved towards posterior margin, continuous from posterior to anterior margins, not merging with lamellar hook, reaching anterior margin of distal lamella above its hook. Capsule orientation: distal lamella seen nearly edge on in capsular view [the view in which greatest detail of the capsule lamellae and lobes can be determined] (Fig. 7B). Capsule lamella (La) broad and terminally rounded (Fig. 7B,D), forming an acute angle to longitudinal axis of capsule; ventral

margin straight (Fig. 7B,D). Distal lobe (Ld) broadly subtriangular; basal margin straight (Fig. 7B,E). Basal lobe (Lb) broad, its internal margins round (Fig. 7B,C). Posterior lamella (Pl) costate and directed distally (Fig. 7B,E).

Adult female (Figs 2C,D; 3E,F; 6B). Measurements (QM-S22452). Carapace; length 7.4, posterior width 8.5; interdistance between anterior lateral eyes 3.9, between posterior lateral eyes 5.0, between median eyes 0.4; diameter of median eyes 0.3. Pedipalp, femur length 8.6, width 3.1; patella length 8.0, width 3.3; chela length 16.6; manus length 9.5, width 5.4, depth 2.9; movable finger length 8.4; fixed finger length 6.2. Metasoma, segment I length 2.3, width 1.8; segment V length 4.3, width 1.3, depth 1.4; vesicle length 4.6, width 1.4, depth 1.4; aculeus length 1.5. Total length 53.0.

Same characters as in males except as follows. Carapace surface almost entirely smooth and minutely pitted, with very few shagreened and granular patches. Tergites predominantly smooth, shiny and minutely pitted, with surface like a subreticulate formation of low ridges forming numerous irregular shallow dimples. Metasoma (Fig. 3E) smooth and minutely pitted, with very few shagreened areas and granules; ventral surface of segments III-V predominantly shagreened. Pedipalp stout and bulky (Fig. 3F); femur length less than $2.5 \times$ the width; patella length less than $2 \times$ the width; chela length less than $3.5 \times$ the width. Pedipalp chela manus less strongly carinated than in males, dorsal secondary carina not discernible. Both halves of genital operculum completely fused, triangular, with posterior extremity truncated, with a shallow median longitudinal suture and a slightly pronounced posterior notch; pectines with 4/4 teeth (Fig. 6B).

DISTRIBUTION. Thornton Uplands, Far North Queensland (Fig. 8).

DISCUSSION

TAXONOMIC CHARACTERS. *Pedipalpal morphosculpture.* The presence of a lobe on the movable finger of the pedipalp chela and of a corresponding notch on the fixed finger is usually indicative of sexual maturity in males and females of the liachelids *Chiromachus*, *Iomachus*, *Hadogenes*, *Opisthacanthus* (subgenus *Nepabellus*) and *Paleochelochtonus* (Prendini, 2000). Subadults lack this feature, which occurs only in the final instar. However, within *Hadogenes*, adult females of some species of the

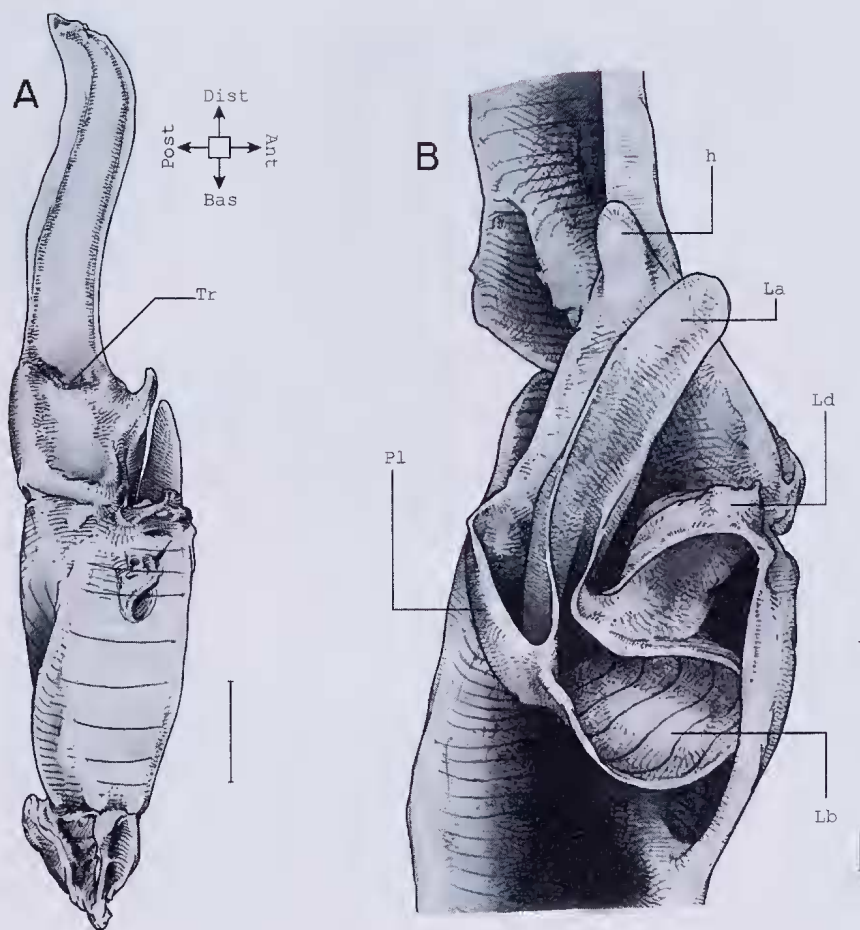


FIG. 7. *Liocheles litodactylus*, male paratype (QMS35475), hemispermatophore. A, hemispermatophore with arrows indicating post-extrusion orientation of the hemispermatophore. Ant (anterior), Bas (basal), Dist (distal), Post (posterior), Tr (transversal ridge). B, detail of the capsular region, internal aspect, h (hook), La (lamella), Lb (basal lobe), Ld (distal lobe), Pl (posterior lobe). Scale lines (A, B) 1 mm.

H. tityrus (Simon) species complex, as well as males and females of *H. zumpti* Newlands & Cantrell, are without any lobe and notch (Newlands & Prendini, 1997). In all previously described species of *Cheloctonus* and *Liocheles* only mature males possess this character, whereas females do not. *Liocheles litodactylus* is the only known representative of the genus in which males possess chela fingers without such a sculpturing on their denticular margins. Sexually mature males of *L. litodactylus* were initially assessed by the presence of fully developed paraxial organs and hemispermatophores (Fig. 7). Despite the highly unusual pedipalpal chela of males, this species is clearly a representative of *Liocheles*, as evidence from other morphological

characters noted above in the diagnoses of the corresponding higher taxa. Prendini (2000: fig. 2) demonstrated that *Liocheles* represents the most derived liochelid and that its monophyly is well supported in contrast to other Liochelidae. The other liochelid genera were placed more basally on all most parsimonious cladograms that he found (Prendini, 2000: figs 2,5,6). Strong evidence of the monophyly of *Liocheles* and of its terminal position in the Liochelidae indicates that the unique pedipalpal morphology of the *L. litodactylus* male represents an autapomorphic loss of the sculpturing found in all other congeneric species.

An additional feature not reported in other species of *Liocheles* is the presence of an irregular cluster

of pale spots (2-4) of glandular appearance, located in the basal half of the external face of the movable finger. Nothing is known about the function of this feature and it is apparently unique to this species.

Sexual Dimorphism. Like in all *liocheles*, the genital operculum of *L. litodactylus* males consists of two separate sclerites which cover a pair of genital papillae, whereas females possess an undivided genital operculum. Secondary sexual characters in which adult males differ from adult females are: more slender pedipalps; stronger granulation of carapace, tergites and metasoma; greater number of pectinal teeth.

BIOGEOGRAPHY AND EVOLUTION

Koch (1977) recognised only three Australian species of *Liocheles* and concluded that *L. waigiensis*, which is widely distributed along the Australian east coast, was a highly variable species. Monod (2000) carried out a revision of all *Liocheles* spp. and pointed out that species richness is much higher than previously reported, especially within the Australo-Papuan *L. waigiensis* complex. Five valid species are known in this group (i.e., *L. extensus*, *L. karschi*, *L. litodactylus*, *L. penta* and *L. waigiensis*), but an ongoing taxonomic study by the senior author indicates approximately 25 distinct forms. Eleven valid species and subspecies of *Liocheles* are recognised worldwide: *L. australasiae australasiae*, *L. australasiae brevidigitatus* (Werner, 1936), *L. australasiae longimanus* (Werner, 1939), *L. davidovi* (Fage, 1933), *L. extensus*, *L. karschii*, *L. litodactylus*, *L. nigripes* (Pocock, 1897), *L. penta*, *L. polisorum* and *L. waigiensis*. Four species, *L. extensus*, *L. karschii*, *L. litodactylus* and *L. waigiensis* are confined to the Australo-Papuan region. With the description of additional new species (mostly from the Australo-Papuan region) imminent, this region seems to contain the greatest diversity. A brief overview follows of the climatological events that most likely shaped the current distribution of

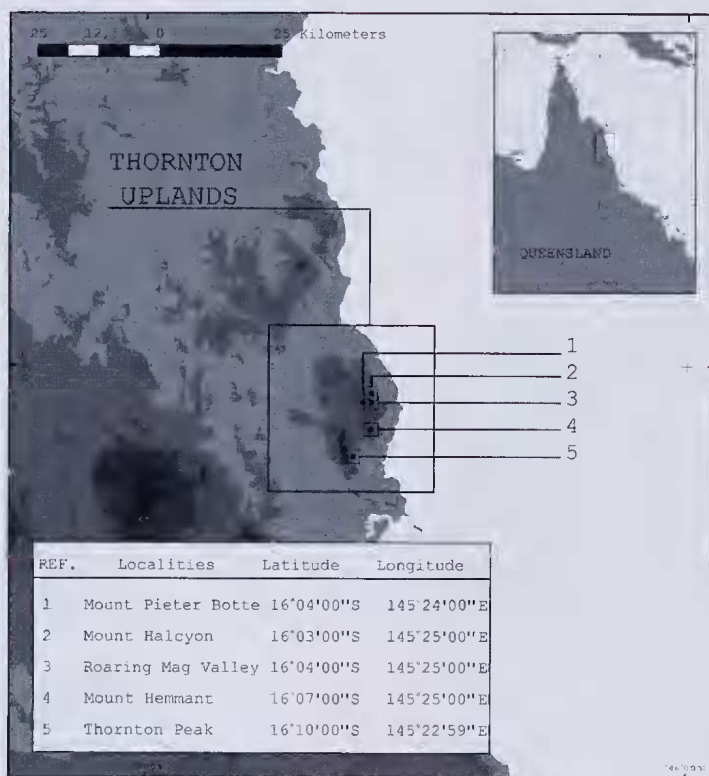


FIG. 8. Map showing the localities of *L. litodactylus* in the Australian Wet Tropics (with a list of localities and their geographic coordinates). Hypsography of the area is represented by graduated grey scale, dark grey representing the highest altitudes. The inset shows the location of the area in Queensland.

habitats in the region and led to the speciation of *L. litodactylus*.

The rainforests discontinuously distributed along the NE coast of Queensland from Cooktown to north of Townsville form a region known as the Wet Tropics. This region consists of a series of isolated mountains and tablelands rising up to 1,600m in altitude, which are surrounded by lowland forests at sea level. The faunal and floral composition of the upland regions (altitude above 300m) is notably different from the lowland mesophyll forest. Nix (1991) described the upland rainforests of the Wet Tropics as a mesotherm archipelago in a sea of tropical lowlands. Fourteen upland rainforest subunits have been recognised (McDonald, 1992; Moritz et al., 2001; Williams, 1997; Williams & Pearson, 1997; Williams et al., 1996; Winter et al., 1984; Yeates et al., 2002).

The rainforests of the Wet Tropics are considered to be remnants of previously widespread

homogenous Tertiary vegetation (Truswell, 1993). Progressive continental drying since the Miocene induced the transformation of the Australian landscape, previously dominated by rainforest, to one dominated by grasslands and woodlands, in which rainforest became very reduced in extent (Kershaw et al., 1994). By the beginning of the Pleistocene the moist area has greatly declined, with rainforest elements segregated along the eastern coast in a similar pattern to that seen today (Adam, 1992). Smaller scale expansions and contractions of rainforest have coincided with recent Quaternary glaciation events (Heatwole, 1987; Kershaw, 1994). During these glacial maxima rainforests within the Wet tropics were replaced by open sclerophyll forests. During the last glacial maximum (between 13000 and 8000 years BP) rainforests contracted to a series of small, fragmented refugia on the highest mountain tops and plateaus, separated by gaps of dryer sclerophyll vegetation (Adam, 1992; Hopkins et al., 1993; Webb & Tracey, 1981).

The occurrence of the *Liocheles* in Australian was thought to be the result of invasion, presumably over land bridges, of ancestral species from Southeast Asia (Koch, 1977, 1981). The most likely route is via a broad land bridge between present day Cape York Peninsula that connected North Queensland and New Guinea during glaciation maxima. After invading Australia from the north, *Liocheles* would have spread southwards in eastern Queensland. However, an ongoing phylogenetic and biogeographic study of *Liocheles* and related genera by the senior author emphasises that the Australian distribution range of *Liocheles* is not a result of dispersal from Asia via New Guinea. Several new findings contradict Koch's view and support the theory that *Liocheles* probably originates from eastern Gondwana (today's Australo-Papuan area) and invaded Southeast Asia after the breakup and dispersion of Gondwana. *Liocheles* was present in Australia well before the glaciation events of the Pleistocene and then was probably widespread in rainforests all over the continent. The repeated climate changes and rainforest contractions that occurred during the Quaternary most likely stranded a population of *Liocheles* on the Thornton Uplands. In which, in isolation from surrounding rainforests (Fig. 7) and gene-flow from conspecifics in neighbouring rainforests, the population evolved allopatrically into the form that is here described as *L. litodactylus*. Isolation of other populations of *Liocheles* on similar 'rainforest islands' in NE

Queensland provides extensive potential for numerous allopatric speciation events. By causing isolation and subsequent radiative evolution of populations of taxa with low powers of dispersal on high altitude refugia (Brühl, 1997), rainforest contractions in the Wet Tropics have enhanced a high degree of 'local endemism' in the region. Consequently several other unrelated taxa show congruent distributions and presumably result from similar vicariance events (Joseph et al., 1995; Schneider et al., 1998; Schneider & Moritz, 1998; Stuart-Fox et al., 2001; Williams, 1997; Williams et al., 1996).

Liocheles litodactylus occurs in highland rainforests of Far North Queensland. We believe that it is locally endemic to the Thornton Uplands, a small mountain massif north of Mossman, for the following reasons:

- 1) All specimens examined were collected in high altitude rainforests above 700 m. This vegetation type is very limited in extent within the Wet Tropics, being restricted to topslopes of granitic highlands (Tracey & Webb, 1975).

- 2) The Thornton uplands was recognised as a biogeographic subregion of the Wet Tropics by Winter et al. (1984) and in subsequent publications by other authors (Williams et al., 1996; Yeates et al., 2002).

- 3) During the past 20 years, the Queensland Museum has conducted numerous surveys of the terrestrial invertebrate fauna of the Wet Tropics (Monteith, 1985, 1995; Monteith & Davies, 1991). Approximately 350 sites were visited and a conscious effort was made to sample every mountain massif more than once over many years. Therefore, the restricted occurrence of this species most probably reflects the extent of the distribution of this species, and is not an artefact of insufficient sampling.

Harvey (2002) defined a short range endemic as a species that is naturally confined to an area of less than 10,000 km². All available evidence indicates that *L. litodactylus* is a short range endemic species that is confined to the Thornton Uplands (an area less than 1,000 km²). *Liocheles litodactylus* is the only Australian scorpion that can be defined as a short range endemic. Ongoing studies on *Liocheles*, and on Buthidae and Urodacidae by the junior author indicate that the Australian scorpion fauna is much richer than currently recognised and that more short range endemic species exist, particularly in northern Australia.

ACKNOWLEDGEMENTS

We are very grateful to the Queensland Museum for providing working space. We are grateful to Robert Raven and Wendy Mackay (Queensland Museum) for access to the Queensland Museum collections and for arranging loans. We also thank Peter Schwendinger, Natural History Museum of Geneva, for constructive comments on preliminary versions of this paper.

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